

Reproductive Variability in *Pediobius alcaeus* (Walker) (Hymenoptera: Eulophidae), a Parasitoid of *Phyllonorycter* (Lepidoptera: Gracillariidae)

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Abstract.—Separate, but sympatric, sexual and asexual populations of *Pediobius alcaeus* (Walker) (Hymenoptera: Eulophidae), a parasitoid of leaf-mining *Phyllonorycter* species (Lepidoptera: Gracillariidae), are shown to exist and to be associated with hosts on different tree species in Britain.

Pediobius alcaeus (Walker) is a solitary koinobiont endoparasitoid of many species of *Phyllonorycter* mining the leaves of deciduous trees and shrubs (Askew & Shaw 1974, 1979). Eggs are laid inside third instar or older host larvae which continue to develop as far as the pupal stage before being killed, and the adult *P. alcaeus* emerge from the host pupae (Askew & Shaw 1979). In Britain, *Phyllonorycter* feeding on *Alnus glutinosa*, *Corylus avellana* and *Quercus* (both *petraea* and *robur*) seem to be particularly liable to attack from *P. alcaeus*, but the chalcidoid is also frequently associated with *Phyllonorycter* hosts on *Fagus sylvatica*, *Malus* spp. and *Carpinus betulus* (Askew 1994).

Our long-standing interest in chalcidoid parasitoids of leaf mining and other insects is, in part, manifested by a records database maintained by one of us (RRA), into which are entered all rearing records from our own field-work, from host collections made by others who submit parasitoids to us for identification, and from reared specimens we have otherwise seen (i.e. all records entering the database are of parasitoids identified by us). As they currently stand, our total records continue to indicate that *Pediobius alcaeus* is exclusively associated with *Phyllonorycter* species mining the leaves of deciduous trees

and shrubs. Our accumulated rearing records of *P. alcaeus* for which sex was scored are given in Table 1: an earlier, condensed compilation giving fewer data was published by Askew (1994), but the rearing records of *P. alcaeus* previously analysed by Askew & Shaw (1974) are not all included in Table 1 as not all of those samples were sexed. For most host species the rearing records of *P. alcaeus* presented in Table 1 come from numerous collections made over a wide geographical spread of localities in Britain and sometimes also continental Europe.

As was first noted by Askew (1975), samples of *P. alcaeus* originating from hosts on different tree genera have one of two distinct categories of sex ratio: either males are well-represented (35-48 per cent), or the sample is virtually entirely unisexual with males comprising at most only about three per cent (Table 1, see also Askew 1994). Samples from *Alnus*, *Carpinus* and *Corylus* are sufficiently large to permit their categorization as host tree genera which support unisexual (female) populations of *P. alcaeus*, whilst bisexual populations are associated with *Betula*, *Fagus*, *Quercus*, *Malus*, *Sorbus* and probably *Acer*. Different *Phyllonorycter* species feeding on the same genus of host plants are attacked by *P. alcaeus* having the same

Table 1. Accumulated total rearing records of *Pediobius alcaeus* (Walker) of known sex (specimens all seen by the authors).

Host plant	Phyllonorycter	Country	<i>P. alcaeus</i>	
			♂♂	♀♀
<i>Acer campestre</i>	<i>sylvella</i> (Haworth)	Britain	1	0
<i>A. platanoides</i>	<i>platanoidella</i> (Joannis)	Britain	0	1
<i>A. pseudoplatanus</i>	<i>geniculella</i> (Ragonot)	Britain	1	0
<i>Alnus glutinosa</i>	<i>froelichiella</i> (Zeller)/ <i>klemanella</i> (Fabricius)	Britain	1	62
		Belgium	0	1
	<i>rajella</i> (Linnaeus)	Britain	0	21
		Netherlands	0	1
		Germany	1	780
		Britain	0	4
<i>A. incana</i>	<i>stettinensis</i> (Nicelli)	Germany	0	43
		Britain	0	20
		Germany	3	135
<i>A. cordata</i>	<i>rajella</i>	Britain	0	4
<i>A. viridis</i>	<i>alpina</i> (Frey)	Switzerland	0	1
<i>Betula</i> spp.	<i>ulmifoliella</i> (Hübner)	Britain	13	26
		Netherlands	3	4
<i>Carpinus betulus</i>	<i>quinnata</i> (Geoffroy)	Britain	6	219
		Netherlands	0	1
	<i>tenerella</i> (Joannis)	Britain	1	4
		Belgium	0	1
<i>Corylus avellana</i>	<i>coryli</i> (Nicelli)	Britain	0	58
		Belgium	0	9
		Netherlands	0	2
		Britain	0	47
<i>Crataegus monogyna</i>	<i>oxyacanthae</i> (Frey)	Britain	0	1
<i>Fagus sylvatica</i>	<i>maestingella</i> (Müller)	Britain	83	107
		Netherlands	2	0
<i>Malus domestica</i>	<i>corylifoliella</i> (Hübner)	Britain	0	1
<i>M. sylvestris</i>	<i>blancardella</i> (Fabricius)	Britain	0	3
		Britain	7	5
		Britain	110	155
<i>Quercus robur/petraea</i>	<i>quercifoliella</i> (Zeller)/ <i>harrisella</i> (Linnaeus)	Britain	110	155
		Netherlands	0	1
		Britain	10	21
		France	2	2
		Netherlands	2	0
			<i>saporiella</i> (Duponchel)	Britain
<i>Salix caprea</i>	<i>salicicolella</i> (Sircom)	Britain	0	1
		Britain	0	2
		Britain	0	1
<i>S. aurita</i>	<i>viminiella</i> (Sircom)	Britain	0	1
<i>Sorbus aucuparia</i>	<i>sorbi</i> (Frey)	Britain	3	2
		Netherlands	1	0

type of sex ratio; further, our limited data indicate that the sex ratio type/host plant relationship probably remains constant across Europe. Careful comparison failed to reveal any consistent morphological differences between *P. alcaeus* from the unisexual and bisexual populations.

In this paper we report the results of

sleeving experiments in which virgin female *P. alcaeus* from either the unisexual or bisexual populations were presented with developing leaf-mines on the parasitoids' own or on an alien host plant. The aims of this investigation were first, to establish the type of parthenogenetic reproduction employed by each of the two pop-

Table 2. Sleeves on *Quercus robur* and *Corylus avellana* into which *Phyllonorycter* species, and later virgin *Pediobius alcaeus* females from varying sources, were introduced. The number of moths and the number and sex of *P. alcaeus* reared in each sleeve are recorded.

Sleeve No.	Host tree	<i>Phyllonorycter</i> species	<i>Pediobius</i> ♀ no. & source	No. of moths reared	<i>P. alcaeus</i> reared
1	<i>Q. robur</i>	<i>quercifoliella</i>	1, ex <i>P. quercifoliella</i>	36	4 ♂♂
2	<i>Q. robur</i>	<i>quercifoliella</i>	1, ex <i>P. coryli</i>	40	34 ♀♀
3	<i>Q. robur</i>	<i>quercifoliella</i>	2, ex <i>Phyllonorycter</i> sp. underside miner on <i>Alnus glutinosa</i>	1	6 ♀♀
4	<i>C. avellana</i>	<i>coryli</i>	2, ex <i>P. coryli</i>	4	29 ♀♀
5	<i>C. avellana</i>	<i>coryli</i>	2, ex <i>P. coryli</i>	14	40 ♀♀
6	<i>C. avellana</i>	<i>nicellii</i>	2, ex <i>Phyllonorycter</i> sp. underside miner on <i>Alnus glutinosa</i>	14	23 ♀♀
7	<i>C. avellana</i>	<i>nicellii</i>	2, ex <i>P. coryli</i>	36	14 ♀♀

ulations, and second, to determine whether the host plant range of the unisexual population could be expanded under artificial rearing conditions.

METHODS

Seven muslin sleeves were fastened to branches of oak (*Quercus robur*) (sleeves 1–3) and hazel (*Corylus avellana*) (sleeves 4–7) in the period 21–25.v.1979. At the same time, or shortly afterwards, reared adult *Phyllonorycter* were introduced. The three *Quercus* sleeves each received two male and two female *P. quercifoliella* (an under-surface miner), whilst six male and three female *P. coryli* (an uppersurface miner) were put into sleeves 4 and 5, and four male and two female *P. nicellii* (an under-surface miner) were introduced to sleeves 6 and 7. Variation in the numbers of moths introduced was partly due to shortage of livestock, but was also experimental against the risk of overstocking sleeves (which might cause leaf abscission as the mines developed).

Virgin female *Pediobius alcaeus* were put in the sleeves during the period 22–25.vi.1979, at which time developing third and fourth instar mines could be seen in most sleeves. The *Pediobius* had been individually reared in tubes and came from three sources: *P. quercifoliella* mines on *Quercus*, *P. coryli* mines on *Corylus* and from under-surface leaf-mines, probably of

P. froelichiella, on *Alnus glutinosa*. One or two virgin *Pediobius* were introduced into each sleeve; their host origins are given in Table 2. Variation in stocking levels was entirely due to shortage of livestock. All host and parasitoid material came from sites in the vicinity of Reading, Berkshire where the experiments were performed.

The sleeves were brought indoors on 10.vii.1979 (sleeves 1–3), 13.vii.1979 (sleeves 4,5) or 1.viii.1979 (sleeves 6,7). All mature and most immature mines were removed and stored separately in plastic boxes for rearing adult insects. When emergence had finished, the numbers and sex of *Pediobius* and numbers of moths produced in each sleeve were recorded.

RESULTS

Despite sometimes heavy leaf abscission due to population explosions of enclosed aphids, mines matured in all sleeves, mostly in good numbers but rather sparsely in sleeve 3. The first *P. quercifoliella*, a leaf under-surface miner, and *P. coryli*, an uppersurface miner, emerged 12–14.vii.1979, whilst *P. nicellii*, another under-surface miner, emerged somewhat later about 2.viii.1979. *Pediobius* also commenced emergence about this latter date. Total emergences of *Pediobius* and moths are shown in Table 2.

DISCUSSION

Sleeve 1, the only sleeve holding *P. alcaeus* from a bisexual population, yielded only male *Pediobius*. This unequivocal result demonstrates that the bisexual population of *P. alcaeus* on *Quercus* produces males parthenogenetically by arrhenotoky, which is usual in haplodiploid Hymenoptera. In contrast the other sleeves, in which *Pediobius* from unisexual populations were introduced to their own or alien hosts, all produced only female *P. alcaeus*. This confirms that the populations which appear to be unisexual from rearing records (Table 1) are indeed thelytokous, and not the result of inseminated females exercising control over fertilisation of their eggs.

The successful parasitization of *P. quercifoliella* on *Quercus*, naturally a host of bisexual populations of the parasitoid, by *Pediobius* originating from unisexual populations on *Corylus* and *Alnus* (sleeves 2 and 3), shows that hosts on the parasitoid's 'wrong' host food-plant can support it under artificial rearing conditions. Also, less surprisingly, *Pediobius* from *Alnus* undersurface mines was reared through undersurface mines on *Corylus* (sleeve 6), and *Pediobius* from uppersurface leaf-mines on *Corylus* was reared through undersurface mines on the same tree (sleeve 7).

Populations of *P. alcaeus* therefore differ in their reproductive biology. The bisexual populations reproduce by haplodiploidy and only males result from unfertilised eggs (arrhenotokous parthenogenesis). Reproduction in the unisexual populations is thelytokous with females developing from unfertilised eggs. It is not clear whether the occasional males appearing in rearings of normally unisexual populations, as on *Alnus* and *Corylus* (Table 1), are the progeny of 'stray' bisexual females, in which case they would presumably be potentially reproductively functional in relation to the bisexual race, or whether they are

progeny of normally thelytokous females, in which case they may be entirely reproductively non-functional.

The situation in *Pediobius alcaeus* is similar in some respects to that pertaining in *Diplolepis spinosissimae* (Giraud) (Hym., Cynipidae) (Plantard *et al.* 1998). This rose gallwasp is thelytokous (up to 4 per cent males) in populations on the Atlantic coast of France, but in two inland populations males comprise 21 and 29 per cent of the populations. The thelytokous populations were found to be infected by the endosymbiotic bacterium *Wolbachia* which prevents the formation of males. Bisexual populations of *D. spinosissimae* were free of *Wolbachia*. Whether or not a micro-organism is implicated in the thelytoky of *Pediobius alcaeus* remains to be determined, but even if this were to be the case, the apparent segregation of sexual and thelytokous populations onto different tree genera, which in *Pediobius alcaeus* occurs sympatrically and (certainly in Britain) consistently, would still require explanation.

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LITERATURE CITED

- Askew, R. R. 1975. The organisation of chalcid-dominated parasitoid communities centred upon endophytic hosts. pp. 130-153. In: Price, P.W. (ed.), *Evolutionary strategies of parasitic insects and mites*, Plenum Press.
- Askew, R. R. 1994. Parasitoids of leaf-mining Lepidoptera: what determines their host ranges? pp. 177-202. In: Hawkins, B.A. and W. Sheehan (eds), *Parasitoid community ecology*. Oxford University Press.
- Askew, R. R. and M. R. Shaw. 1974. An account of the Chalcidoidea (Hymenoptera) parasitising leaf-mining insects of deciduous trees in Britain. *Biological Journal of the Linnean Society* 6: 289-335.
- Askew, R. R. and M. R. Shaw. 1979. Mortality factors affecting the leaf-mining stages of *Phyllonorycter* (Lepidoptera: Gracillariidae) on oak and birch. 2.

Biology of the parasite species. *Zoological Journal of the Linnean Society* 67: 51–64.

Plantard, O., J.-Y. Rasplus, G. Mondor, I. Le Clainche, and M. Solignac. 1998. *Wolbachia*-induced thelyt-

oky in the rose gallwasp *Diplolepis spinosissima* (Giraud) (Hymenoptera: Cynipidae), and its consequences on the genetic structure of its host. *Proceedings of the Royal Society B* 265: 1075–1080.